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BULLETIN
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The Genus *Frankia* in the United States.

By GEO. F. ATKINSON.

(PLATE CXXVIII).

At the Indianapolis meeting of the A. A. A. S. in 1890, Dr. W. J. Beal exhibited before the Botanical Club specimens of root-galls on *Ceanothus Americanus*.* Knowing of my interest in the subject of root-galls he left the specimens with me for determination. The galls resembled so closely in external appearance those of the tubercles of some of the Leguminosæ that I half suspected they were caused by a similar organism. On examining a section, however, it was at once apparent that the analogy was entirely superficial. In the parenchymatous tissue surrounding the central cylinder were numerous enlarged cells occupied by what appeared to be plasmodia, bearing a striking resemblance to those of *Plasmodiophora Brassicæ*, Wor.†

Fearing that the real nature of the organism might be disguised by the influence of the alcohol in which the specimens were preserved, I sent to Dr. Beal for fresh material. From this material the true condition of affairs was at once presented. The organism is closely allied to that producing the galls on the roots of various species of *Alnus* and the Elæagnaceæ, which has been long known in Europe, and was first described by Woronin as *Schinzia Alni*.‡ This fact, and also that the fungus has more

* Botanical Gazette, Vol. XV., No. 9, p. 232.

† Pringsheim's Jahrbücher, Bd. XI., 1877.

‡ Ueber die bei der Schwarzerle und der gewöhnlichen Garten-Lupine auftretenden Wurzelanschwellungen, Memoires d. l'Acad. Imp. d. Sciences, VIIe Series, Tome X., No. 6, p. 2, 1866.

recently served as the basis of Brunchorst's new genus *Frankia*,* I reported to the Botanical Club at the Washington meeting of the A. A. A. S., 1891.†

During the month of December following I took occasion on one of my collecting trips to examine the roots of *Alnus serrulata*, believing for more than a year that quite likely the fungus was as common here as in Europe. This I found to be the case, and I have since collected some very fine specimens. The next step was to examine the roots of *Ceanothus Americanus* in this vicinity, and sure enough the galls are common to Alabama as well as to Michigan, and I have no doubt that a rich harvest has for years been awaiting the root-gall fungus hunter in all parts of America.

On *Ceanothus Americanus* the galls when young are flesh colored, cylindrical, and from 1-2 mm. in diameter, by 2-6 mm. in length. They originate as minute lateral abnormal growths from young roots, or in many cases from the side of the large tap root. In successive years they continue their growth by a dichotomous or trichotomous branching, each year's growth remaining from 1-2 mm. in diameter and 4-6 mm. in length. After several years there is developed a loosely branched dendroid body. The older portions of the gall become dark or nearly black in color, while the new year's growth is flesh color.

The galls on *Alnus serrulata* differ in form as a whole, while the manner of growth is quite similar. The individual yearly growth is more restricted, so that a rotund or irregularly oval more or less compact mass with a botryose appearance is developed. The gall of the first year is 2-3 mm. long by 1-2 mm. in diameter. By successive di- or tri-chotomies the mass is formed from the size of a pea to that of a small walnut. In some species of *Alnus* the gall reaches the size of one's fist.‡ In the larger galls on the *Alnus* the original dichotomous branching is lost sight

* Ueber einige Wurzelschwellungen, besonders diejenigen von *Alnus* und den Elæagnaceen, Unters. Bot. Inst. Tübingen, Zweiter Band, p. 151. u. folg.

† Botanical Gazette, Vol. XVI., No. 9, p. 262.

‡ Woronin, Mem. de l'Acad. Imp. des Sciences ; Sorauer, Pflanzenkrankheiten, Zweite Auflage, Erster Band, p. 747. Brunchorst, Unters. Bot. Inst. Tübingen ; Frank, Krankheiten der Pflanzen, and others.

of in the compact growth, and is only plainly visible in the surface.

The internal structure of the gall differs but little in the relation of the different tissue systems from that of the normal root. The central cylinder is present surrounded by an abnormally great development of parenchymatous tissue, which is surrounded by the corky layer. The parenchymatous tissue harbors the parasite.

In *Ceanothus Americanus* there is a narrow zone of parenchymatous cells, immediately surrounding the central cylinder, usually free from the parasite and made up of nearly isodiametric cells. Bordering this is a broad zone of parenchymatous tissue of large cells quite variable in size and shape. The cells containing the parasite are usually considerably larger than the others. Frequently all the cells of this zone viewed in cross section are elongated radially. In *Alnus serrulata* the cells containing the fungus are but little if any larger than the other parenchymatous cells, and the radial elongation of the cells is rarely observed. The observation and determination of the fungus is not so easy as in the galls on *Ceanothus Americanus*, because of other substances which obscure it.

The fungus when mature forms compact botryoid clusters in the affected parenchymatous cells of the gall, the central portion being composed of a complexly-branched mass of threads bearing at their ends on the periphery of the mass the globose sporangia.

A brief résumé of the leading views concerning these galls from a historical standpoint will be of interest in connection with a description of the fungus.

Meyen* considered them to be parasites growing upon the roots of *Alnus*, having a habit in this respect similar to members of the Balanophoraceæ or Orobanchaceæ, though lower in development and systematic position.

Schacht† at first regarded them as normal growths of the roots. Later‡ he held the view that they were abnormal growths, but offered no theory as to their cause.

* Ueber das Hervorwachsen parasitischer Gewächse, etc., Flora, 1829, S. 49. Quoted from Woronin, Mem. d. l'Acad. Imp. d. Sciences VIIe, Tome X., No. 6, p. 2.

† Flora, 1853, S. 10, 11. Quoted from Wor. l. c.

‡ Der Baum, 1860, S. 172-174. Quoted from Wor.

Jäger * thought they were of insect origin.

Woronin † considered the fungus to be closely related to Nägeli's genus *Schinzia*. This genus was founded upon a fungus which pierced the root rind of various species of *Iris*, and produced flask-shaped bodies at the ends of the threads in the cells‡.

Magnus considered it too different from *Schinzia cellulicola* to be placed in the same genus.§

An article by A. Gravis || entitled, "Observationes anatomicæ sur les excroissances des racines de l'aune" induced Woronin to make additional researches upon young galls of *Alnus*. The condition of the organism he found here bore such a resemblance to his *Plasmodiophora Brassicæ* * that he communicated to Gravis his belief that two organisms were frequently present, one a *Plasmodiophora* like Myxomycete, and the other a filamentous fungus. Gravis communicated this in "Note sur les excroissances des racines de l'aune.†"

E. Warming ‡ notes the presence of galls on *Hippophaë*, *Elæagnus* and *Shepherdia* which resemble those on *Alnus*, and records the discovery of what he considers a parasitic Myxomycete of like nature with Woronin's *Plasmodiophora*.

H. Möller§ in his earlier studies of these galls used only alcoholic material, and probably for this reason overlooked the real nature of the fungus. He claimed to have demonstrated

* Ueber eine krankhafte Veränderung der Blüten Organe der Weintraube, Flora, 1860, S. 49. Quoted from Woronin.

† Mem. d. l'Acad. Imp. d. Sciences, VIIe, Tome XI., No. 6, 1866, St. Petersburg.

‡ Flora, 1842, p. 278. See Sorauer, Pflanzenkrankheiten, Bd. I., p. 748.

§ Sitzungsberichte des bot. Ver. d. Prov. Brandenburg XXI., June 27, 1879. Quoted in Sorauer, Pflanzenkrankheiten, Bd. I., p. 748.

|| Bulletin de la Société royale de Botanique de Belgique, Tome XVIII., 1re partie, p. 50-60. See Berichte der Deutschen Botanischen Gesellschaft, Bd. III., 1885, p. 177.

* Pringsheim's Jahrbücher Bd. XI., 1877.

† Compte rendu de la séance mensuelle du Jan. 10, 1880, de la Société royale de botanique Belgique. See Berichte der Deutschen Botanischen Gesellschaft Bd. III. 1885, p. 177.

‡ Smaa biologiske og morfologiske Bidrag. Botanisk Tidsskrift, 3de Række, Bd. I., 1876, p. 84. Reference "Wurzelknöllchen bei den Elæagmeen, Just's Jahresbericht, 1876, p. 439.

§ *Plasmodiophora Alni*, Berichte der Deutschen Botanischen Gesellschaft, Bd. III, 1885, p. 102-105.

its affinity with *Plasmodiophora* and named it *Plasmodiophora Alni*. Woronin* then reviews Möller's article and states that it yet remains to be shown whether this *Plasmodiophora*-like parasite is the sole cause of the root galls, or whether, perhaps, as he already had suggested† it was accompanied by a filamentous fungus.

Brunchorst,‡ by his excellent investigations, gets the key to the true nature of the parasite and thus fairly sets in order a subject hitherto clouded in great confusion. The fungus is shown to be a filamentous one and what Woronin§ and Möller|| took to be spores are in reality sporangia, which by successive oblique divisions of the protoplasmic contents form spores.

The plasmodia of various authors is the cell plasma of the host with the very fine fungus threads imbedded in it and so obscured that they cannot be seen except by the use of certain reagents. Thus with the use of a hot solution of "Salzsäure" in galls from *Alnus glutinosa*, a delicate filamentous structure, reminding one of a skein of matted threads, is made visible.

In longitudinal sections of a gall, he calls attention to three rather ill-defined zones, representing different stages of development of the parasite. Just behind the root-cap is the first zone, bearing the younger stages of the fungus, where in fresh untreated preparations it resembles plasmodia. Next comes the sporangium zone, where the hyphæ can be seen quite well, bearing on their ends at the outer surface of the hypha-skein the sporangia. In the third zone the contents of the sporangia are either undergoing division into spores, or are empty.

The likeness of the fungus in the younger zone to plasmodia

* Berichte der Deutschen Botanischen Gesellschaft, Bd. III., 1885, p. 177, 178.

† Compte rendu de la séance mensuelle du 10 Jan., 1880, de la Société royale de botanique Belgique. See also Revue Mycologique, Tome II., 1880, p. 69, 70, and Bot. Centralblatt, 1880, p. 354.

‡ Ueber die Knollchen an den Wurzeln von *Alnus* und den *Eleagnaceen*. Bot. Centralblatt, xxiv. p. 222, 1885.

§ Ueber einige Wurzelanschwellungen, besonders diejenigen von *Alnus* und den *Eleagnaceen*. Unters. Bot. Inst. Tübingen, Zweite Band, p. 151, 1886. See also Bot. Centralb. Bd. xxviii, p. 109, 1886.

|| Mem. Acad. Imp. Sci., etc.

|| Bericht., Deut., Bot. Gess.

is heightened by the fact that the threads which emerge from the mass and pass through the cell walls to other cells, give the appearance of very delicate pseudopodia.

Ward * says that the fungus of the tubercles of the roots of Leguminous plants stimulates the protoplasm of the tubercles, so that it resembles plasmodia. It is possible that some such influence is exerted on the protoplasm of the galls of *Alnus*, etc.

Woronin,† Frank,‡ Sorauer § represented several sporangia on a single thread. Brunchorst (l. c.) shows that this appearance is an optical illusion, sporangia frequently lying over threads appear as if united with them.

Möller|| observed the hyphæ in the sporangium zone, but regarded them as remnants of the plasmodium, which did not go to form spores and which remained in connection with the spores as they were differentiated from the mass. Brunchorst calls attention to the fact that if this were so they would not be so constant in outline and diameter.

Brunchorst properly regards the fungus as distinct from *Schinzia*, and takes it as the type of a new genus which he calls *Frankia*. Unfortunately he does not accept the well-known specific name *Alni*, but calls it *Frankia subtilis*. While there are variations in the size of the sporangia from different hosts, he does not consider them sufficient to be of specific value.

Thus in *Alnus undulata* they vary from 4μ - 6μ ; in *Hippophœ rhamnoides* from 2μ - 3.5μ ; and in *Alnus glutinosa* from 3μ - 5μ .

B. Frank * rejects the theory that they are abnormal growths due to a parasitic fungus, but regards them as normal organs for the transitory storage of proteid bodies.

Möller,† in 1890, reinvestigated the galls, using fresh material

* Phil. Trans. Vol. 178, p. 547.

† Mem. d. l'Acad. Imp. d. Sci. VIIe. T. X. 6, 1866.

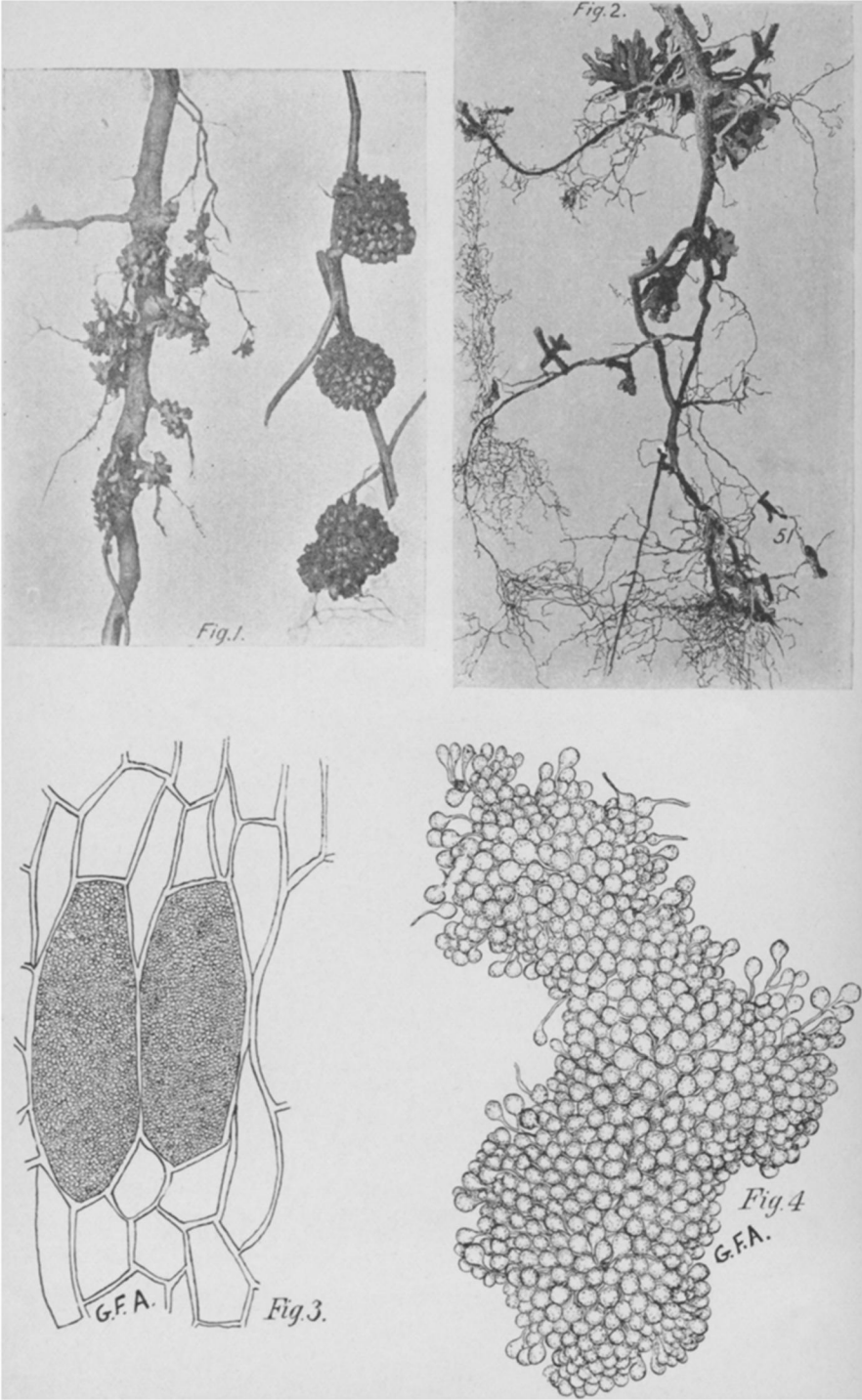
‡ Krankheiten der Pflanzen, 647.

§ Pflanzenkrankheiten, Bd. I.

|| Ber. d. Deutsch. bot. Gesellschaft Bd. III. 1885, p. 102.

* Sind die Wurzelschwellungen der Erlen und Elaeagnaceen Pilzgallen? Ber. d. deutschen Bot. Gesellschaft, Bd. V. Heft. 2. Reference in Bot. Centralblatt, Bd. XXV. p. 366.

† Beitrag zur Kenntniss der *Frankia subtilis* Brunchorst, Ber. d. Deutsch. bot. Gesellschaft Bd. VIII., 1890, p. 215-224. See Centralblatt für Bakteriologie und Parasitenkunde Bd. VIII., 1890, p. 559-560 and Bot. Centralb. 1891, p. 60.



FRANKIA ALNI (Wor.) and F. CEANOTHI, Atkinson.

instead of alcoholic material, and corroborates Brunchorst's view that the organism is a filamentous fungus, but differs from him in some minor details. Brunchorst thought the hyphæ were septate, but Möller claims that they are continuous.

He also notes the much stouter mycelium and the irregular sporangia in the galls of *Myrica Gale*, and considers it a distinct species for which he proposes the name *Frankia Brunchorstii*.

It appears to me that the fungus in the galls of *Ceanothus Americanus* is a distinct species from the other forms, and I propose the name *Frankia Ceanothi* for it.

In addition to the characters given above are the following: The infected cells are $30-50 \times 50-70 \mu$. The sporangia are smaller than in any described species, varying from $1.5-2 \mu$.

It is worthy of remark, probably these organisms have a very wide and complete distribution, so that the galls are probably found wherever the hosts grow. In this respect they are analogous to the organisms which produce the tubercles on the roots of the Leguminosæ. The question would then naturally arise whether there is a symbiotic relationship between parasite and host, for so far as can be seen they cause no inconvenience to their host. I am not aware that this matter has been tested. The contents of the sporangia of *Frankia*, like the "bakteroids" of the tubercles, have a proteid nature* and color yellow with Jod, red with Millon's reagent, and are tinged easily with hæmatoxylin and aniline colors as eosin and methylviolet.

I would be pleased to receive these root galls on any plants, from any parties who would be kind enough to look for them on any shrubs. The host plant should in all cases be given and the roots well wrapped in peat moss or other damp packing material to keep them fresh.

EXPLANATION OF PLATE CXXVIII.

Fig. 1.—*Frankia Alni* (Wor.), root galls on *Alnus serrulata*.

Fig. 2.—*Frankia Ceanothi*, Atkinson. root galls on *Ceanothus Americanus*.

Fig. 3.—Same, group of parenchymatous cells showing two containing fungus.

Fig. 4.—Same, showing cluster of sporangia more highly magnified. The cluster has been removed from the cell.

Phytopathological Laboratory, Alabama Polytechnic Institute,
Auburn, Ala., April 14, 1892.

* Brunchorst, Unters. Bot. Inst. Tubingin. 1886. B. Frank, Bericht. d. Deutsch. Bot. Ges. V. 2.